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VOL. XXVII. NO. 6.

STUDIES IN MORPHOGENESIS.

IV.

A PRELIMINARY CATALOGUE OF THE PROCESSES CONCERNED IN ONTOGENY.

BY C. B. DAVENPORT.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
NOVEMBER, 1895.

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No. 6. — Studies in Morphogenesis. — IV. A Preliminary Catalogue of the Processes concerned in Ontogeny.[1] By C. B. Davenport.

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Most important perhaps of all the problems which the biologist sees lying unsolved before him is that of the development of the individual, — a problem to which, from the time of Aristotle, zoölogists have repeatedly turned, although scarcely hoping for its eventual solution.

Without attempting to consider the various theories of Ontomorphogenesis which have at different times been offered, it is sufficient to state that it is now generally agreed that ontogenesis is a process, or rather a complex of processes, taking place in the protoplasm of the developing individual.

Now it is a highly probable belief that no movement takes place in protoplasm except as a response to stimuli. The very fact that ontogenesis is a complex of actions indicates that there must be a large number of stimuli raining in upon the different parts of the developing protoplasm to which they respond.

In order to gain some idea of what the stimuli are, it is first necessary to analyze the ontogenetic complex of processes into its simple elementary ones.

It is the aim of this paper to make such an analysis into the elementary ontogenetic processes as a basis for determining the nature of the exciting stimuli.

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. L.

91251

Other authors have devoted chapters to "Developmental Processes," but none of these can be considered as at all complete.

Thus O. Hertwig, in his "Text-Book of the Embryology of Man and Mammals" (English Translation by E. L. Mark, 1892, p. 76), has a "General Discussion of the Principles of Development." He recognized two main ones: (1) the principle of unequal growth (producing folds which are either invaginations or evaginations, and which may unite along their edges); and (2) the principle of histological differentiation.

Minot, in his Human Embryology, in a chapter on "Differentiation," seems to think also that these two processes are sufficient to explain the differentiation of organs.

More important in this connection than either of the preceding is the recent paper of Herbst in the "Biologisches Centralblatt" (Vol. XIV. Nos. 18–22). This author, after reviewing the literature upom taxism and tropism, explains as phenomena of the same order certain ontogenetic processes. He has not, however, attempted to catalogue all the ontogenetic processes.

Before beginning the present catalogue, I may state that I distinguish between ontogenetic *principles* and ontogenetic *processes*. Under the first head I include such laws of development as terminal growth, repetition of parts and bilateral symmetry in development. These I have not attempted to catalogue. The present paper is concerned only with the latter group, which comprises the different elementary operations or actions exhibited in ontogeny.

These may be divided into two classes: 1. the grosser ontogenetic processes; and 2. histogenic processes. This paper deals with the first class only.

In discussing the grosser ontogenetic processes we may distinguish (A) those of a more general nature from (B) the more special ones.

A. The *general ontogenetic processes* comprise those of a general physiological character. Of these, at least three are commonly recognized:—

1. Growth (including both the results of assimilation and of imbibition of water).
2. Nuclear division.
3. Secretion.

B. The *special* ontogenetic processes are differential in character, i. e. the differentiation of the body is effected by them.

These processes may be classified, first of all, according to the form of

the protoplasmic bodies in which they occur. These exist either as (I.) isolated cells, or as larger multinucleated bodies. Of the latter we may recognize three classes: (II.) bodies extended chiefly in one direction, — threads, fibres, tubules; (III.) those which extend as a layer; and (IV.) those in which the three dimensions are more nearly equal, forming solid masses.

I propose now to discuss the processes occurring in each of these four classes.[1]

I. Ontogenetic Processes occurring in Migratory Protoplasmic Bodies — Mesenchyme.[2]

1. *Migration of Nodal Thickenings in a Protoplasmic Mesh-work.* This process is found, for example, in many Arthropod eggs before the formation of the peripheral blastoderm. (Figure 1.) No one can doubt that protoplasm extends throughout the whole egg in the form of a mesh- or foam-work, whose interspaces are filled with yolk. The protoplasm is aggregated around the nuclei at certain nodal points, which later migrate to the surface or through the yolk as vitellophags. Cf. K. & H.,[3] Figs. 7, 363, 417, 448, 472, 473, 771.

Fig. 1.

[1] It may be a cause of dissatisfaction to some that this classification is not "strictly dichotomous"; it is still more serious that the different heads are not of co-ordinate rank or mutually exclusive. Of course, the classification employed in this list cannot be regarded as a final one. I hope, however, that I have succeeded in an attempt roughly to arrange the different items in a logical fashion.

[2] In the present paper the word "mesenchyme" is used as a name for all amœboid, migrating cells, of whatever origin.

[3] Throughout this paper certain abbreviations are used in referring to the books from which the figures are copied. These are: K. & H. for Korschelt und Heider's "Entwicklungsgeschichte"; M. for Minot's "Human Embryology"; and H.-M. for Hertwig's "Text-Book of Embryology of Man and Mammals," translated by Mark.

Fig. 1. Section through an egg of a Myriapod (Geophilus), showing the nodal thickenings (*n. t.*) in the act of migrating towards the periphery of the egg. See K. & H., Fig. 449.

2. *Free Migration of Amœboid Bodies.* This process differs from the preceding in that the migrating bodies are not connected together. It is characteristic of mesenchyme. I know that Dreyer ('92, Jena. Zeitschr., XXVI. 359) and Sedgwick ('94, Quart. Jour. Micr. Sci., XXXVII.) insist that the cells of mesenchyme, which are usually considered unconnected like so many amœbæ, are really nodal thickenings in an extensive mesh-work or foam-work, the intervening fluids being the, in some places confluent, vacuoles. Wherever mesenchyme has this structure, its migrations belong to the preceding class. But I believe there still remains a considerable residuum of cases falling under this head.

This process is capable of division into two subprocesses; viz. (*a*) migrating of mesenchyme out of a protoplasmic layer in order to become free, and (*b*) migrating through fluid-filled spaces. Both these processes are illustrated in Figure 2. Further illustrations will be found in K. & H., Figs. 102, 103, 170, 175–180, 182, 186, 188–190, 207, 285, 559, 596–598, 628, 698, 733, 809, and M., Figs. 121, 234, 239.

FIG. 2.

The migratory processes named below are of subordinate rank to Nos. 1 and 2. But, being fairly well marked and of considerable importance, it is convenient to treat them as co-ordinate.

We may distinguish, first, movements of mesenchymatous elements towards and from each other, and, secondly, movements with reference to other protoplasmic masses.

3. First among the former we recognize the *aggregation of migratory protoplasmic bodies*, and here we may distinguish three sub-classes according to the form of the resulting body.

a. First we have the *aggregation of mesenchyme into a body with a chiefly linear dimension*, — the formation of a thread, cord, or tubule.

Examples of this process in Invertebrates are seen in the formation of the kidney of Lamellibranchs, which seems to be laid down as a cord-like aggregation of mesenchyme, and in that of the thread of the yolk glands

Fig. 2. Section of Holothurian larva showing mesenchyme migrating out of a layer at *a*, and through a fluid-filled space at *b*. From H.-M., Fig. 109.

of Turbellaria according to Iijima (Zeitschr. f. wiss. Zool., XL. 455). Among Vertebrates, we have the observations of Paterson, (Figure 3,) according to which the sympathetic nerve arises by the aggregation of mesenchymatous elements into a strand; of His, who affirms the origin of the spinal and the olfactory ganglia from migrating cells; and of various authors, who make blood capillaries and lymph vessels arise by this process (cf. M., pp. 217, 413).

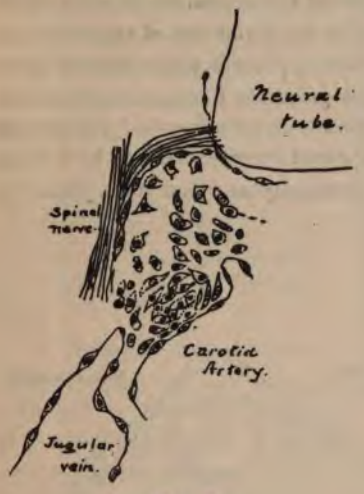

FIG. 3.

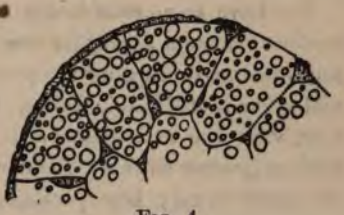

FIG. 4.

FIG. 5.

b. Next we must consider the *aggregation of mesenchyme into a superficially extended body,* — the formation of a layer. This process does not seem to be very common; one example is seen in Figure 4.

c. As the last of these processes of aggregation we have the case of *aggregation into a mass.* This wide-spread ontogenetic process may be illustrated by the formation of gemmules in a marine sponge (Figure 5). Other examples are found in the formation of the adductor muscles of

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Fig. 3. Cross section of a rat embryo in the upper thoracic region, showing the development of the sympathetic nerve (between spinal nerve and carotid artery). From A. M. Paterson, '91, Trans. Roy. Soc. Lond., Pl. XXII. Fig. 4.

Fig. 4. Later stage of the embryo shown in Figure 1. The migrating protoplasm has aggregated itself into a layer at the surface of the embryo. See K. & H., Fig. 449.

Fig. 5. Section of a marine sponge (Esperella), showing a gemmule, a mass of aggregated mesenchyme which is about to produce a gemmule (1'), and migrating, not yet aggregated mesenchyme (1). After H. V. Wilson ('94, Jour. of Morph., IX. Pl. XIV.).

Lamellibranchs, the muscles of the foot of Gastropods (K. & H., Fig. 556, *s. m.*), and the lymph glands and spleen of Vertebrates (M., p. 414).

The reverse process to the aggregation of mesenchymatous cells is their *Dispersal*, and this has probably been brought about by the opposite cause to that producing aggregation. Since, however, this is a process taking place in a protoplasmic *mass*, its consideration must be deferred. (See page 194.)

We have been considering the different forms into which mesenchymatous elements aggregate themselves in the formation of one body; it now remains to consider the processes taking place between mesenchyme and other protoplasmic bodies. Of these processes I recognize at present four, viz.: the attachment of mesenchymatous cells to a body, following their migration thither; the encapsuling and interpenetration by a mass of mesenchyme; transportation by mesenchyme; and absorption by mesenchyme.

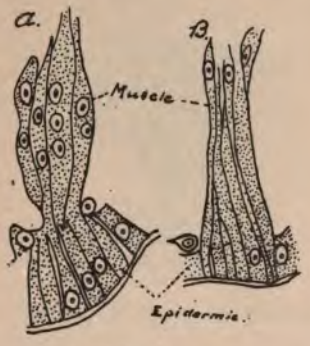

Fig. 6.

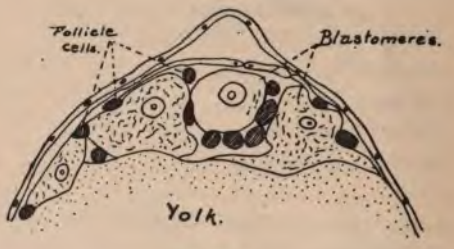

Fig. 7.

4. *Attachment of Mesenchyme* to another body. This process occurs in the union of the muscles of Lamellibranchiata, Annelida, Crustacea, and Bryozoa (Figure 6) to the hard parts of these animals, and of tendon to bone, in Vertebrates.

5. *Investment and Interpenetration, by Mesenchyme*, of a mass — either some other organ of the body or a foreign substance, like a parasite — is a not uncommon process. Especially marked is this process in the Tunicata (Figure 7), where migrating follicle cells encapsule and finally

Fig. 6. Sections through the body wall of the Bryozoan, Paludicella; (*a*) young, (*b*) adult; illustrating the process of attachment of mesenchymatous muscles to the cuticula.

Fig. 7. Section of the germ disk of Pyrosoma, showing migrating follicular cells surrounding the blastomeres. (See K. & H., Fig. 771.)

penetrate between the blastomeres, so that it is difficult to tell which part of the embryo has been derived from the egg and which part by immigration. Compare the origin of the cutis in Echinoderms (K. & H., Fig. 195), in Mollusca (K. & H., Fig. 686), and in Vertebrates (M., Fig. 306), and of the intestinal and vascular musculature of Vertebrates (H.-M., Fig. 185).

All of these processes have this in common, that mesenchyme migrates to an organ — vessel, layer, or mass — and applies itself closely to it, sometimes even penetrating into the substance of the organ.

6. *Transportation by Mesenchyme* has hitherto been observed in but few cases. The most remarkable instance of this process is found in the Doliolidæ, where the buds produced from a stolon are transported over half the length and half the circumference of the body by means of mesenchyme cells, and are finally deposited, in very regular order, on the appendage of the budding individual. (Figures 8 and 9.) By similar means, apparently, one end of the funiculus of the Bryozoan Cristatella is transported from the dorsal to the ventral surface of the corm, as I have attempted to show elsewhere. (Bull. Mus. Comp. Zoöl., XX. 142.)

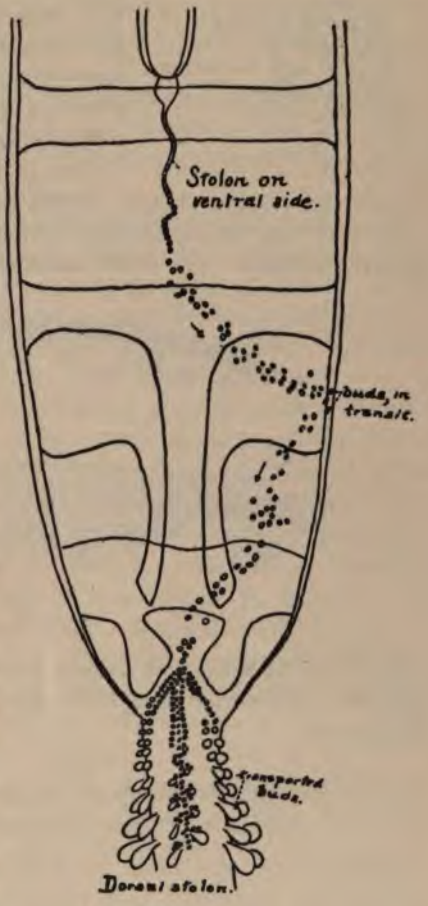

FIG. 8.

Fig. 8. Dorsal view of the posterior part of a large Doliolum "nurse." Shows the buds being transported from the ventral to the dorsal (and posterior) stolon. (See K. & H., Fig. 830.)

7. Absorption by Mesenchyme. Only of late years have we come fully to appreciate the great rôle played in ontogeny by the devouring capacity of mesenchyme. It is now fully established that such migratory protoplasmic bodies — phagocytes — are the most important agent in the degenerative processes which larvæ undergo in their metamorphoses.

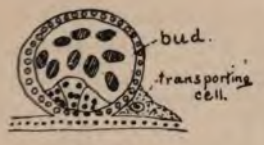

FIG. 9.

This is well shown in Insects (Figure 10), in Bryozoa probably, in Ascidians, and in the frog.

The secreting activity of mesenchyme has already been classed under general processes. No doubt mesenchymatous cells perform various

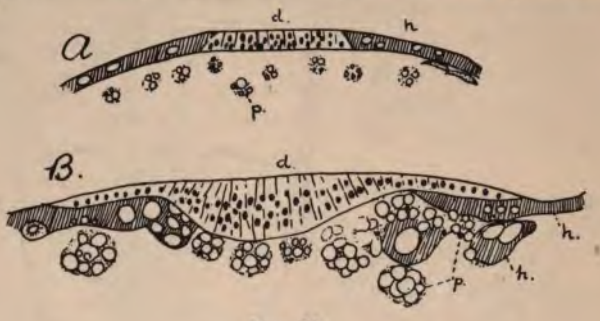

FIG. 10.

other functions in the body besides transportation, digestion, and secretion, but these either have little effect on the form or concern only histogenesis.

II. ONTOGENETIC PROCESSES OCCURRING IN ELONGATED PROTOPLASMIC BODIES — FIBRES, THREADS, CORDS, TUBULES.

Falling under this head we may recognize, first, certain general changes due to growth, such as increase in length or in thickness. These may affect either the whole body or its parts, and may lead to a diminution or increase in size.

Fig. 9. Section through the transported bud of Dolchinia, showing the amœboid transporting cell. (See K. & H., Fig. 839.)

Fig. 10. Sections through the abdominal imaginal disks of the hypodermis of Musca. *A*, from the larva. *B*, from the young pupa. In *B* the phagocytes (*p.*) are in the act of devouring the larval hypodermis (*h.*), which is replaced by the superficial growth of the imaginal disk (*d.*). K. & H., Fig. 530.

We may recognize, in the second place, certain processes which concern the *direction* which the elongated body takes and its *relation* to other bodies of the same or of a different kind. This latter group is the only one which requires further analysis and illustration. Vacuolization of cords, such as occurs in blood-vessels, will be considered in Section IV.

In this section we may consider four processes: (1) tropic processes, including the turning of elongated bodies towards or from any object; (2) the splitting of such bodies; (3) their anastomosis; and finally (4) their fusion with other organs.

1. *Turning of Elongated Protoplasmic Bodies towards or from an Object.* This is a process which has long been recognized by botanists as occurring in roots and stems, and as being a response to a stimulus coming from outside the organism. Also among hydroids the position of stolons and hydranths is often clearly determined by external stimuli. Of organs inside of the body, the determination of the direction of growth of nerves has been referred by Herbst to the action of a stimulus supplied by the organ towards which the nerve grows. Other examples of this process are not rare. I will cite a few. Herbst has already referred to the case in Turbellaria where unicellular glands of mesenchymatous origin send out long processes (the necks), which gain their appropriate connections with the other organs. So, too, the shell-gland of Crustacea, which arises from an aggregation of mesenchyme (K. & H., p. 377) secondarily sends out a stalk which makes connection at the appropriate place. The principal blood-vessels of Vertebrates arise in the area vasculosa and subsequently grow into the embryo, following certain prescribed paths (M., pp. 215, 216). From these vessels others in turn bud out, progressing towards their destined organs. According to Field ('91, Bull. Mus. Comp. Zoöl., XXI. 222), the pronephric duct of Amphibia, arising in mesoderm, grows at its posterior end, secondarily fusing with the cloaca. Again, the tubules of the metanephros, according to some authors, bud out of the blind end of the ureter, and in their further growth hit exactly the independently formed Malpighian capsules lying in the mesenchyme. In all these cases we have the elongating body clearly turning towards the object with which it is destined to unite.

Even under some abnormal conditions we have this process taking place; for instance, when a parasite lodges in any organ of a Vertebrate, new vessels are formed, which grow out towards the source of irritation. (Cf. Roux, '81, Der Kampf der Theile, pp. 150, 151).

2. *Splitting of an Elongated Protoplasmic Body* (cord or tubule). We may recognize here two sub-processes: (*a*) splitting at the tip, and (*b*) splitting along the whole length.

a. As is well known, nerves grow out as blunt stalks which repeatedly divide at their ends. Paterson has shown that some of the spinal nerves split at the somato-splanchnic angle, as shown in Figure 11. His ('88,

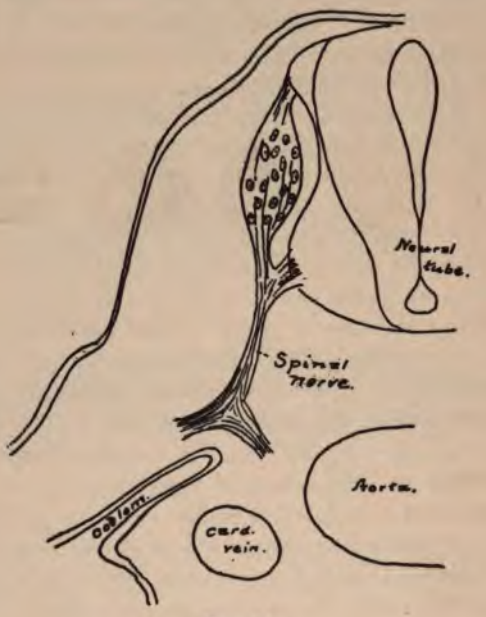

FIG. 11.

Arch. f. Anat., Jahrg. 1887, p. 376) shows in many cases that the splitting takes place where the end of the growing nerve strikes a rigid organ. Thus, he says, when the third branch of the trigeminus strikes Meckel's cartilage, it divides into the ramus lingualis and the ramus mandibularis; and when the hypoglossal meets the jugular vein, it divides into its descending and lingual branches. The way in which the rigid organs act to produce splitting is thus explained by His. Pre-existing resistant objects may be considered as the "Motivs" of division; for as a nerve

Fig. 11. Cross section of a mouse embryo in the lumbar region, showing the splitting of the spinal nerve at the upper angle of the cœlom. After Paterson, '91, Trans. Roy. Soc. London, CLXXXI., Fig. 5.

stem strikes a cartilage or a vessel, its fibres are bent in different directions and the stem divides. The resisting objects are thus considered by His to act in a mechanical, i. e. *direct* way. The results are, however, equally explicable by the response-to-stimulus theory.

The splitting which occurs at the blind ends of developing blood-vessels and excretory tubules, and the repeated divisions of many glands — salivary gland (M. Fig. 334), liver, and lungs (M., Fig. 445) — are examples of this process. Other cases are found among Invertebrates, as, for example, the tentacles of many Cnidaria (K. & H., Figs. 27, 31), "roots" of Sacculina, and liver branches of Limulus (K. & H., Fig. 338).

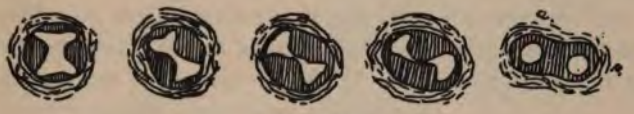

FIG. 12.

b. The second case, that of division of a tubule throughout its entire length, is illustrated in the development of the segmental duct in some Vertebrates, and in the separation of aorta and pulmonary artery. (Figure 12).

3. *Anastomosing*, or the process of fusion of similar threads, thus forming a network, is of wide-spread occurrence. It is exemplified in the development of nerves (Figure 13) and blood-vessels in Vertebrates, and in some glands, especially the vertebrate liver.

4. *Fusion with other Organs.* The process of fusion of diverse organs will be studied in greater detail in other sections of this paper. It occurs, for instance, at the close of the process of growth of the neck of a mesenchymatous gland (or other independently arising tubule) towards its insertion.

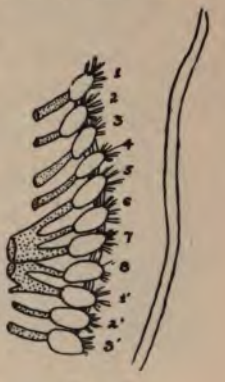

FIG. 13.

Fig. 12. Sections at different levels through the cardial aorta of a human embryo of 11.5 mm. The lowest section is at the left; the highest at the right: the separation progresses from above downwards. *a*, aorta; *p*, pulmonary artery. See M., Fig. 293.

Fig. 13. The cervical and three of the thoracic spinal nerves of a human embryo, showing the origin of the thoracic plexus. See M., Fig. 360.

III. Ontogenetic Processes occurring in Protoplasmic Layers.

The ontogenetic processes occurring in protoplasmic layers may concern one layer only, or two or more layers acting in relation to each other.

The processes which take place in one layer are principally growth processes affecting on the one hand the *area*, on the other the *thickness* of the layer.

III[a]. Of the growth processes affecting *area*, we may distinguish (α) such as take place in the walls of a hollow sphere or cylinder from (β) such as take place on a plane or warped surface.

a. The areal growth occurring in a hollow sphere or cylinder (sac) may be equal in all the axes or elements of the wall, leading merely to a change of size of the sac; or it may be unequal in the various axes or elements, producing a change in form. It is this latter group which especially interests us, and it will therefore be further analyzed.

Fig. 14.

1. We may recognize three cases in the differential growth processes occurring in a sac: (*a*) unequal growth in the different axes; (*b*) unequal growth at the poles of the axis; (*c*) unequal growth in the various meridians of the sac.

These three processes deserve illustration.

a. By the process of excessive growth in a certain axis we have the ellipsoidal form produced from the spherical; as in the Sycandra larva (Figure 14); in planulæ (K. & H., Figs. 14, 30, 32, 51); in the larvæ of various worms (K. & H., Figs. 144, 158, 159); in the Echinoid blastula (K. & H., Figs. 173, 176); and in the larvæ of some Mollusca (Figs. 542, 576, 593, 596) and Bryozoa (Fig. 702).

b. Through unequal growth at the two poles of (e. g. the chief) axis, we have produced such ovoidal forms as planulæ, in which not only is the chief axis elongate, but one pole has grown more than the other. (Figure 15.) By unequal growth at the poles are produced also such

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Fig. 14. Sycandra embryos. *A*, 8-cell stage; *B*, larva. See K. & H., Figs. 2 and 3.

club-shaped pouches as the "club-shaped gland" of the Amphioxus larva (K. & H., Fig. 875).

c. Through unequal growth of the different meridians of a spheroidal or cylindrical wall we have produced from the spheroid an apparent flattening on one face, such as occurs, for example, in various cases of "epibolic gastrulation." In Figure 16 this process is illustrated in the spheroidal egg of a Heteropod. (Cf. K. & H., Figs. 66, 541, 738.)

FIG. 15.

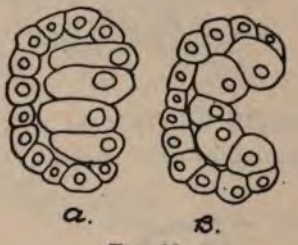

FIG. 16.

By an excess of growth along the meridians of one side of a cylinder we have produced such apparent rotations of the internal organs as occur in Crinoids and Endoprocta. (K. & H., Figs. 218, 732.)

β. Let us now consider the unequal areal growth of a part of a bounding layer taken so small that it may be considered as nearly a plane or a warped surface. We shall find that the processes taking place in such a part are among the commonest and most important of all occurring in ontogeny.

This unequal growth may result, either (2) in parts formerly lying in one plane moving into different planes; or (3) in parts formerly lying in one line moving out of that line.

2. It has long been recognized that, when in a layer excessive growth takes place over a restricted area, the result is that the excessively enlarged area can no longer occupy its former territory. Since its periphery remains relatively constant while the included layer increases

---

Fig. 15. Section through the planula of Æquorea, to show the greater expanse at one pole than at the other. See K. & H., Fig. 14.

Fig. 16. Sections through young embryos of Firoloides, showing how the condition in stage *B* has been derived from that of stage *A* by greater growth along the meridians on the left than on the right. See K. & H., Fig. 584.

in area, the latter is compelled to fold, producing, according to the point of reference, an elevation above or a depression below the general level.

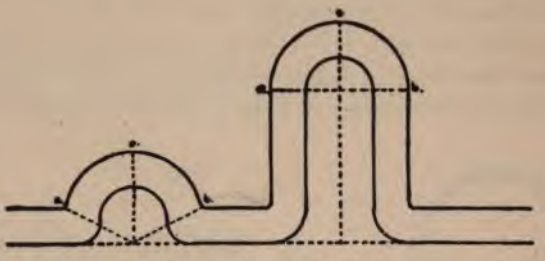

FIG. 17.

So important relatively is the process of folding that it has apparently been regarded by some authors as almost the sole developmental process. How important a rôle it plays is well illustrated in Figure 18, where (excepting the nerve masses and the heart, which are unrepresented) all of the differentiated organs of the squid which at this stage lie in the sagittal plane are represented. And these are seen to have arisen by the foldings of the unilaminar blastoderm which covers the yolk. The connections of the otocyst and the shell-gland with the exterior are now lost, but fin, mantle margins, funnel, and the various appendages of the alimentary tract, as well as the tract itself, are all seen to be arising as foldings of the blastoderm. This view does

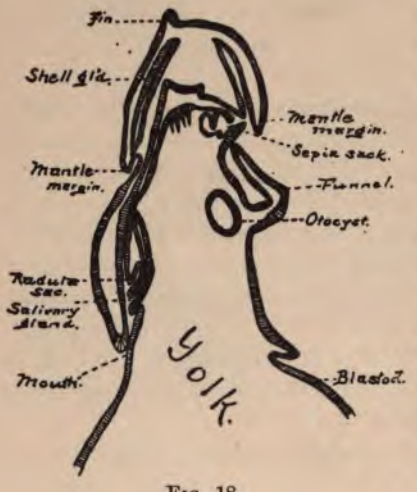

FIG. 18.

Fig. 17. Diagram representing the process of folding as it occurs in protoplasmic layers. By excessive growth between *a* and *b*, the fold *a o b* is produced.

Fig. 18. Sagittal section of an embryo of Loligo vulgaris, showing the origin of organs through foldings of the blastoderm. From K. & H., Fig. 673.

not include the lateral organs, — eye vesicles, gills, and arms, — which arise in a similar fashion as folds.

Based upon the form of the growing area, two classes of folds may be recognized: —

(*a*). *Pockets*, from a circular area.

(*b*). *Linear folds*, from an elongated area.

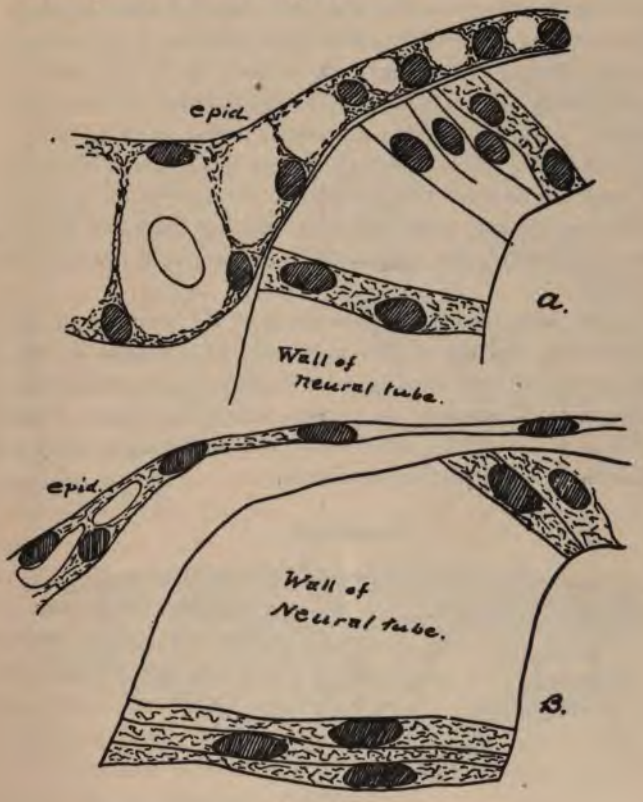

FIG. 19.

Good examples of the formation of pocket folds are seen in many cases of gastrulation, and in the otocyst, shell gland, salivary gland, and sepia sac of Figure 18.

Fig. 19. Two stages in the development of the epidermis and neural tube of the chick. Both magnified to the same extent. (From W. His, '94, Arch. f. Anatomie, Jahrg. 1894, pp. 74, 76.)

Typical linear folds occur in the formation of the neural tube of most Vertebrates, of the lateral line of fishes, and of the atrium of Amphioxus. (K. & H., Fig. 881.)

3. Inequalities of growth in different parts of the layer may take place, so that parts originally lying in a line move out of that line. By this means are produced folds lying in the plane of the layer, — folds comparable to those made by an advancing wave front on entering a bay. Such folds may occur in the *bounding line* of the growing layer, as happens, it is alleged by some, in the overgrowth of the yolk by the blastoderm, — a process by which the crescentic notch is produced on the edge of the blastoderm. Again, such folds may occur in the *midst* of a layer, producing a relative displacement of the points lying in that layer. To this process may be referred the remarkable rotation of the gill slits and mouth of Amphioxus, — the gill slits rotating from the right to the left side of the larva, the mouth from the left side towards the mid-ventral line.

III[b]. The processes affecting thickness of the layer are of very common occurrence, and are of two kinds, — (4) processes leading to an increase, and (5) those leading to a diminution in thickness. These variations in thickness may be general, extending over a considerable part or the whole of the area under consideration, or they may be restricted to a small part of that area.

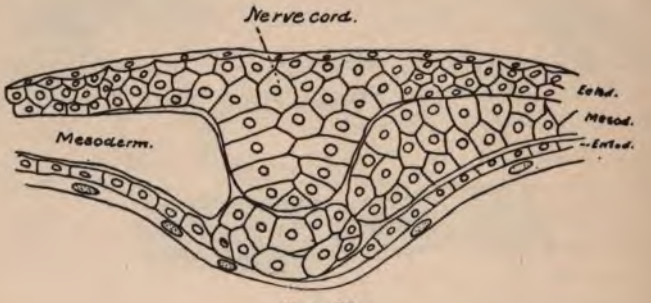

FIG. 20.

4. The process of thickening is illustrated in the lateral walls of the neural tube of Vertebrates (Figure 19), and, localized, in the formation of the neural tube in Teleosts (Figure 20). Other examples are seen in

Fig. 20. Cross section of the blastoderm of a bony fish (Serranus atrarius) to show the linear thickening of the ectoderm to produce the nerve cord. (From H. V. Wilson, '91, Bull. U. S. Fish Commission, IX. Plate XCV.)

the papillæ which precede the formation of feathers, and in the ingrowing follicles which form hairs.

5. A general thinning of the walls of the organs is found to accompany the development of many Invertebrates. Figure 21 illustrates this fact.

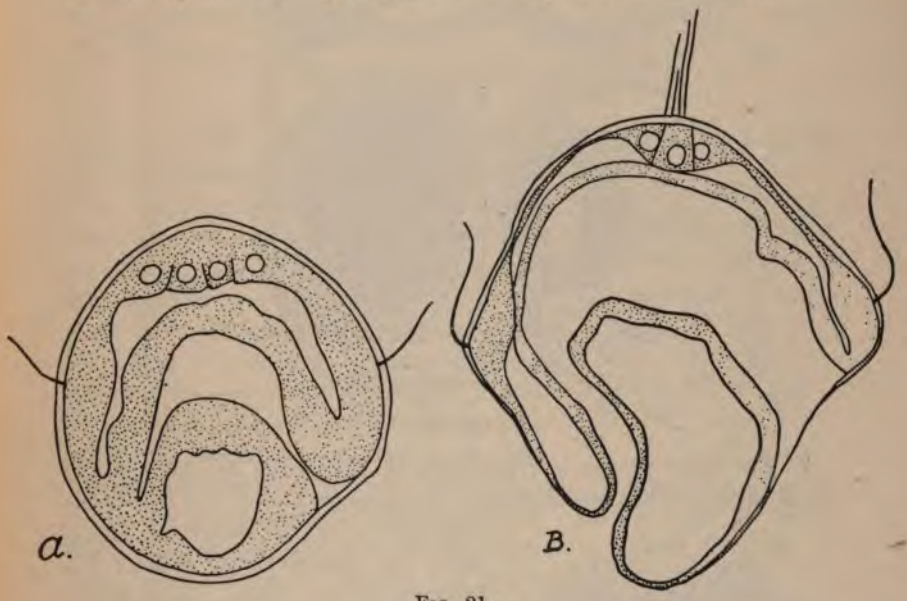

FIG. 21.

In Figure 19 a general thinning of the epidermis is seen in passing from stage α to stage β. A good example of local thinning is seen in the formation of the ependyma of the roof of the brain and medulla.

The processes of thickening and thinning may go on side by side, as in the formation of the lens of the vertebrate eye (Figure 22), where the outer and inner layers of the lens are at an early stage of nearly equal thickness, but where, in the later stages, the outer layer becomes thin, and the inner layer enormously thick.

III^c. Next, we must consider the processes by which a single continuous layer experiences an interruption in its continuity. This may take place (6) by a complete *atrophy* of a part of the membrane, thus forming a hole or rift in it, or (7) by a separating off of a certain piece from the membrane.

Fig. 21. *A*, younger, and *B*, older Trochopore stages of the annelid Eupomatus uncinatus, seen in sagittal section. Drawn to same scale. Outlines copied from Hatschek, '86, Arb. Zool. Inst. Wien, VI. See also K. & H., Fig. 118.

6. The former process occurs typically in the ontogeny of reptiles, and perhaps of mammals, where the middle of the layer of "primary entoderm" roofing the yolk cavity atrophies, making a great hole in the layer.

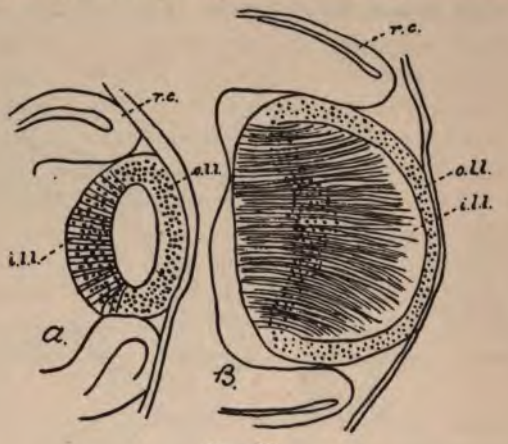

FIG. 22.

7. The latter process is represented in Hatschek's familiar figure of the formation of the neural tube of Amphioxus (Figure 23), where the medullary plate is shown as falling below the general level without the intervention of a fold. Compare the formation of the "body plate" of the Nemertine Lineus, K. & H., Fig. 105, and gastrulation in Apis, K. & H., Fig. 495.

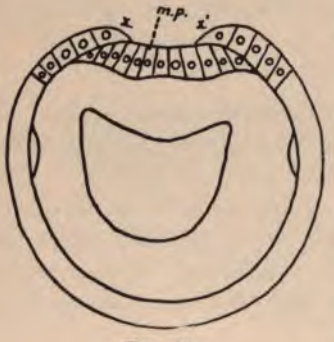

FIG. 23.

III[d]. Finally, we must consider the important processes involving two or more protoplasmic layers. Such layers may move either towards or from each other. We will here consider only the former group of cases.

8. The mutual approach and fusion of layers may be called *con-*

Fig. 22. *A*. Section of eye of chick embryo on third day. (See M., Fig. 413.) *B*. Section of eye of rabbit embryo, 13 days old. (See M., Fig. 409.) *i. l. l.*, inner lens layer; *o. l. l.*, outer lens layer; *r. c.* retinal cup.

Fig. 23. Section across an Amphioxus embryo, showing the medullary plate, *m. p.*, which has sunk below the level of the ectoderm, producing a discontinuity in the latter. From H.-M., Fig. 69.

crescence. We may distinguish three sub-processes under this head,

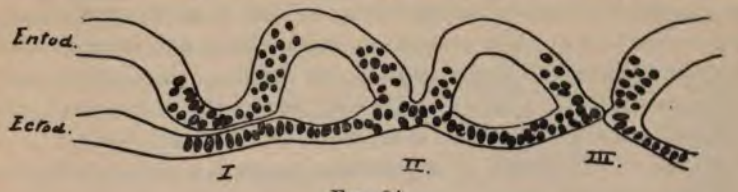

FIG 24.

depending upon whether (*a*) the concrescence takes place along the free margins of layers, or (*b*) along their surfaces, or, finally, (*c*) along the edge of folds. This concrescence is usually quickly followed by other processes which we will consider later.

a. The concrescence of layers by their free edges is illustrated in the cases of the growing together of the free edges, x and x', of the ectoderm in the Amphioxus embryo at a stage a little later than that shown in Figure 23. (K. & H., Fig. 504.)

b. The concrescence of layers flatwise is illustrated in the formation of the vertebrate mouth when the anterior end of the entodermal sac comes in contact with the ectoderm. Likewise in the formation of the gill slits of Vertebrates the broad bottoms of the entodermal sacs move to the ectoderm. (Figure 24, I, II.)

c. Concrescence along the edges of two folds is perhaps the commonest of these three forms of concrescence. It is that by which in Vertebrates the neural tube is closed (Figure 25, *A*, *B*, *C*); ectodermal

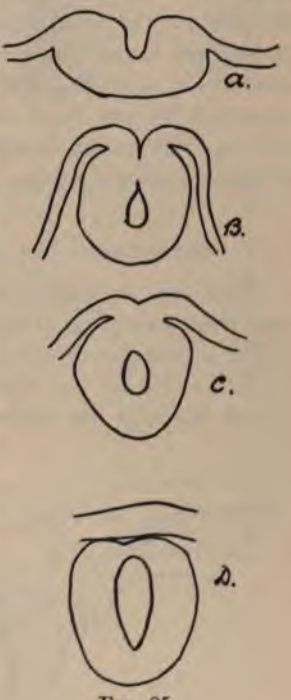

FIG. 25.

Fig. 24. Part of a frontal section through an embryo of Acanthius vulgaris, of about the stage of Balfour's Stage I. Shows 3 stages in the formation of the gill slit, I, II, illustrating *concrescence* of layers flatwise; III, *perforation*. Original. From a preparation kindly lent me by Mr. H. V. Neal.

Fig. 25. Cross sections through the neural tube of embryo frogs of different ages, showing the concrescence of the lips of the medullary groove (*A*, *B*, *C*), and (*D*) the final separation of the upper and lower layers of the fold. After H. H. Field, '91, Bull. Mus. Comp. Zoöl., XXI. No. 5.

pockets, like the lens and otocysts, become transformed into closed sacs; and grooves, like those of the lateral line, become transformed into canals. In Invertebrates also this process is a very common one, being exemplified in the closure of the blastopore, in the closure of the amniotic cavity in Insects (K. & H., Figs. 474, 475, 484), and in the formation of optic and otic vesicles generally (K. & H., Figs. 377, 630, 681–683).

The end of the process of concrescence proper is a *fusion* of the two concrescing layers, whether the concrescence is occurring along free edges, flatwise, or along the edges of folds. (Fig. 25, *C*, Fig. 24, II.)

9. Frequently this process is followed by another one; viz. the *perforation* of the fused layers (Fig. 24, III), or the *separation* of the upper and lower components of the folds when two folds have been concrescing (Fig. 25, *D*). By means of *perforation* the two spaces separated by the fused walls are put into communication with one another. By means of *separation* a pocket becomes a closed sac, and a groove becomes a tube.

IV. Ontogenetic Processes occurring in Protoplasmic Masses.

These may be classed into three categories according as the most *prominent* change produced is (IV^a) in volume, (IV^b) in form, or (IV^c) in number of masses.

IV^a. 1. Under the first group are included changes produced by *growth* which is not uniform in all parts. Thus the growth may be prevailingly along one axis, by which means a cylindrical mass is derived from a spherical one (embryos of Dyciemidæ, K. & H., Fig. 99), or it may be excessive at one pole (gemmules of sponges, H. V. Wilson, '94, Jour. of Morphol., IX., Pl. XVI.), or along one meridian. Again the growth may be more localized, being confined to a small area or to a line; as, for instance, in the case of the mesodermal core of the appendages of Arthropods (K. & H., Fig. 371), and of Vertebrates (Figure 26, "limb-bud"). By

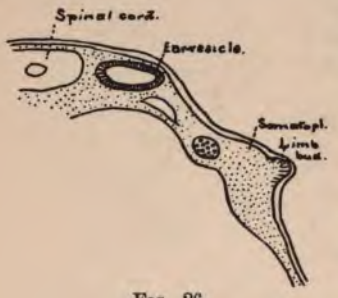

Fig. 26.

Fig. 26. Cross section through embryo of a Teleost, Fundulus, showing origin of the pectoral limb-bud as a solid outgrowth of the somatopleure. After E. R. Boyer, '92, Bull. Mus. Comp. Zoöl., XXIII. No. 2, Fig. 58.

this process of localized solid growths the principal differentiations of Phanerogams occur.

IV^{b}. 2. An important change of form of a protoplasmic mass may occur independently of growth by a *rearrangement of the nuclei* of the mass.

FIG. 27.

Good examples of this process are found in the development of the larva of Lucernaria (Figure 27); in the development of Ctenophores (K. & H., Fig. 67); and in the changes of form occurring in the "ectodermal basal plate" of Salpa (an apparent syncytium), according to the figures of Heider ('95, Abh. Senckenberg. naturf. Ges., Bd. XVIII. Figs. 32, 40, 41). In so far as this process involves the migration of nuclei, it is clearly closely related to Process I. 1.

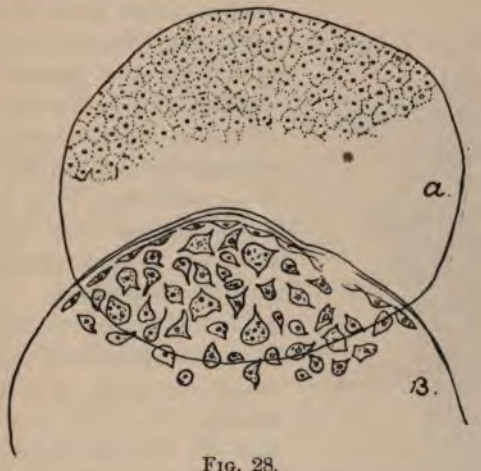

FIG. 28.

Fig. 27. *A*, *B*, *C*, are three successive ontogenetic stages of Lucernaria. The transformation from stage *B* (36 nuclei in the section) to stage *C* (33 nuclei in the section) is due to a rearrangement of the nuclei. See K. & H., Fig. 49.

Fig. 28. *B*, dispersal of elements of the gemmule *A*, which was formed, as illustrated in Figure 5, by the aggregation of similar mesenchymatous elements. This process precedes the development of the gemmule into a larva, and accompanies the imbibition of water by the gemmules. After H. V. Wilson, '94, Jour. of Morphol., IX., Plate XVI.

3. Another way in which the mass changes form without growth is by *vacuolization*. Through vacuolization there arise, e. g., the blastula in many eggs, the secondary body cavity in many Invertebrates (K. & H., Fig. 131, 689), and in Bryozoa the cavities of the bud. This process of vacuolization, which I introduce for convenience at this place, is not confined to masses. Many cords by vacuolization (canalization) become tubules, and many layers become divided into two. Of vacuolated *cords*, I need refer only to the formation of capillaries in Vertebrates and of nephridia in Invertebrates; of vacuolated *layers*, to the origin of the cœlom in most Vertebrates. In all cases, the acquisition of a mass of water at the centre causes a rearrangement of the nuclei.

4. Perhaps this is the most fitting place to mention the process of *Dispersion* of elements, which occurs not only in bodies originally formed by aggregations of mesenchymatous elements (Fig. 28), but also in *layers* having an epithelial origin, e. g. the ectoderm of Distomum. (K. & H., Fig. 88.)

IV^c. The remaining processes occurring in protoplasmic masses are of such a nature as to alter the *number* of masses. We can distinguish, correspondingly, two classes: the first including such as have to do with the formation of two masses from one, through division; the second including those which have to do with the union of two masses into one. The first, then, are *division* processes; the second, *fusion* processes.

Fig. 29.

5. Under the first head we may include the process of *constriction*, by which two more or less independent masses arise from one. An illustration of this is found in the case of embryonic fission described for some Bryozoa by Harmer (Figure 29). Closely allied to this is the process of sloughing off of a part of the body in metamorphosis, one of the most striking instances of which is shown in

Fig. 29. Section through a brood chamber of Crisea eburnea, showing the constricting off of secondary embryos from the primary embryo. After Harmer, '93, Quart. Jour. Mic. Sci., XXXIV., Plate XXIII. Fig. 11.

Sacculina, where the thorax and abdomen are thrown off, the head alone persisting to complete the metamorphosis.

FIG. 30.

6. Another division process is that of *splitting* of the mass. This is illustrated by the case of the optic mass of the lobster (Figure 30), which splits into an outer and an inner part. Compare the origin of the nervous system of Peripatus, K. & H., Fig. 442, B.

7. Under the second head, *fusion* of contiguous masses, we may place such cases as that of the union of independently arisen ganglionic masses, such as Morgan describes for the Pantopod, Pallene (Figure 31).

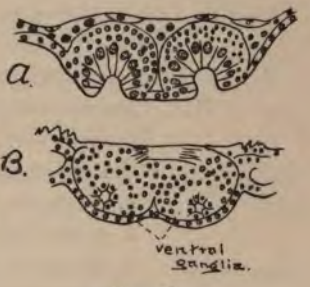

FIG. 31.

Fig. 30. Sections through three stages in the development of the compound eye of the lobster after G. H. Parker. In *B* and *C* the mass is seen to be splitting into the retina and optic ganglion. See K. & H., Fig. 263.

Fig. 31. Ventral part of sections across Pallene embryos. *A*, earlier stage, showing the paired neural invaginations; *B*, later stage, ganglia fused. See K. & H., Figs. 409, 410.

Recapitulation and General Remarks.

We may now, in recapitulation, arrange in tabular form the differential processes which we have recognized.

I. Processes occurring in *mesenchyme.*
  1. Migration of nodal thickenings, p. 175.
  2. Free migration of amœboid bodies, p. 176.
    a. from a layer.
    b. through fluid-filled spaces.
  3. Aggregation of mesenchyme, p. 176.
    a. into a thread.
    b. into a layer.
    c. into a mass.
  4. Attachment of mesenchyme, p. 178.
  5. Investment and interpenetration, p. 178.
  6. Transportation, p. 179.
  7. Absorption, p. 180.

II. Processes occurring in protoplasmic *threads* or *tubules.*
  1. Tropism, p. 181.
  2. Splitting, p. 182.
  3. Anastomosing, p. 183.
  4. Union with other organs, p. 183.

III. Processes occurring in protoplasmic *layers.*

III^{a}. Processes affecting *area.*

α. Processes occurring in the wall of a sac.
  1. Excessive growth of particular parts, p. 184.
    a. along one axis.
    b. at one pole.
    c. along one meridian.

β. Processes occurring in a plane or warped surface.
  2. Formation of perpendicular folds, p. 185.
    a. Pocket folds.
    b. Linear folds.
  3. Formation of folds in the plane of the area, p. 188.

III^{b}. Processes affecting *thickness.*
  4. Thickening, — general or local, p. 188.
  5. Thinning, — general or local, p. 189.

III^{c}. Processes affecting *continuity.*
  6. Atrophy, p. 190.
  7. Detachment of a piece from a layer, p. 190.

III[d]. Processes affecting *two or more layers.*
8. Concrescence, p. 191.
a. of free edges.
b. of surfaces.
c. of edges of folds.
9. Perforation, p. 192.
IV. Processes occurring in protoplasmic *masses.*
IV[a]. Effecting especially change of *volume.*
1. Excessive growth of particular parts, p. 192.
b. general.
c. local.
IV[b]. Effecting especially change of *form.*
2. Rearrangement of nuclei, p. 193.
3. Vacuolization, p. 194.
4. Dispersion of elements, p. 194.
IV[c]. Effecting especially change in *number.*
5. Constriction, p. 194.
6. Splitting, p. 195.
7. Fusion, p. 195.

The processes here ennumerated may be for the most part grouped under three general heads: —

I. Taxic processes.
II. Tropic processes.
III. General growth processes.

Under *Taxic Processes* I include such as are accompanied by free migration of protoplasmic bodies, or by the flowing of protoplasm from one part of the whole body to another part.

Under *Tropic Processes* I include such differential growth processes as result in a turning of protoplasmic bodies (threads or folds) towards one another or towards another protoplasmic body.

By *General Growth Processes* I mean those differential growth processes which are not included under tropic processes.

To the category "taxic processes" may be provisionally assigned Nos. I. 1, 2, 3, 4, 5, and 6; III. 4 (in part) and 5 (in part), 7 (?), 9; IV. 2, 4, 5, 6, 7.

To the category "tropic processes" may be assigned Nos. II. 1, 2, 3, 4; III. 8, 9.

To the category "general growth processes" may be assigned Nos. III. 1, 2, 3, 4 (in part) and 5 (in part), 6; IV. 1 and 3.

It will be noted that No. I. 7 (absorption by mesenchyme) is not assigned to any one of the three categories; and that certain other processes (III. 7, Detachment from a layer; II. 2, Splitting; III. 4 and 5, thickening and thinning of a layer; and IV. 3, Vacuolization) are of so doubtful a nature that, although assigned to the special categories, this assignment can be regarded as provisional only.

The process of absorption does not readily fall into one of the three categories, and at the same time it does not seem worth while to erect a special category for it.

As for the doubtful cases, the doubt is not whether they are referable to one of these categories, but rather in knowing in which one to place them.

Regarding the three general categories, it has long been recognized that taxic and tropic processes are responses to stimuli. It has not been so generally recognized that all growth processes are such. A moment's consideration will, however, make this probable.

Let us consider for a moment what it is that controls differential growth, — What makes one part of a membrane grow faster than another, causing a folding of that part?

Inequality of growth is clearly not due to inequality of food supplied, since folds arise in uniformly nourished membranes, — bathed, that is to say, uniformly by the nutritive fluids. It must therefore be due to inequality of the activities which lead to growth; namely, the taking in of food and its assimilation, and the imbibition of water. Now it is our fundamental assumption that activities of all sorts, including ingestion and imbibition, are responses to stimuli. In so far, then, as differential growth is dependent upon the inequality of these activities in different parts of the membrane, it is dependent upon stimuli acting upon that membrane.

Whenever the activities are diverse in the different parts of a membrane, it must be either that the stimulus applied to the different parts is diverse, or, if not, that the protoplasm is diverse in its different parts, for what the result shall be depends upon two factors, — the quality of the stimulus and that of the protoplasm.

Let us now consider somewhat more in detail the taxic and tropic processes. As is well known, the stimuli which control these movements result either in migration towards the source of the stimulus or away from it, so that positive or negative taxis or tropism occurs. In ontogeny it is often impossible to say where the source of stimulation is, and therefore whether the tactic or tropic movements are + or —. Cer-

tain criteria may, however, be employed in some cases to determine this. Thus, where many migratory bodies move towards a common point, or where a thread or tubule makes its way to a distant point, we may believe that a positively tropic stimulus is exercised by that point. Also, where two similar parts move towards each other, it is probable that a + stimulus is exerted by both; where, on the other hand, they mutually withdraw, it is probable that a mutual negative stimulus emanates from both.

With these criteria in mind we may classify some of the taxic and tropic processes as + or —, and this I have attempted to do in the following table: —

Probable Responses to Positive Stimuli.	Probable Responses to Negative Stimuli.
Taxic.	*Taxic.*
I. 3. Aggregation of mesenchyme.	I. 2, *a*. Migration from a layer.
I. 4. Attachment of mesenchyme.	III. 4. Thinning of a layer (when due to flowing of the protoplasm from a point).
I. 5. Investment and interpenetration.	III. 9. Perforation.
I. 6. Transportation.	IV. 4. Dispersal of elements.
III. 4. Thickening of a layer (when due to flowing towards one point).	IV. 5, 6. Separation of masses.
IV. 7. Fusion of masses.	
Tropic.	
II. 1. Turning of thread.	
II. 3. Anastomosing.	
II. 4. Union with other organs.	
III. 8. Concrescence.	

Probable Responses to either + or — Stimuli.

I. 1. Migration of nodal thickenings.
I. 2, *b*. Free migration of amœboid bodies.
IV. 2. Rearrangement of nuclei.

It is not too much to believe that the foregoing hypothetical interpretation of the ontogenetic processes lies within the possibility of experimental test. Just as the control of the migration of amœboid bodies in the adult has been undertaken with success, so may we hope to control the tropic and aggregation phenomena of ontogeny. By *experiment* alone can the causes of the developmental processes be determined.

Cambridge, Mass., May 1, 1895.

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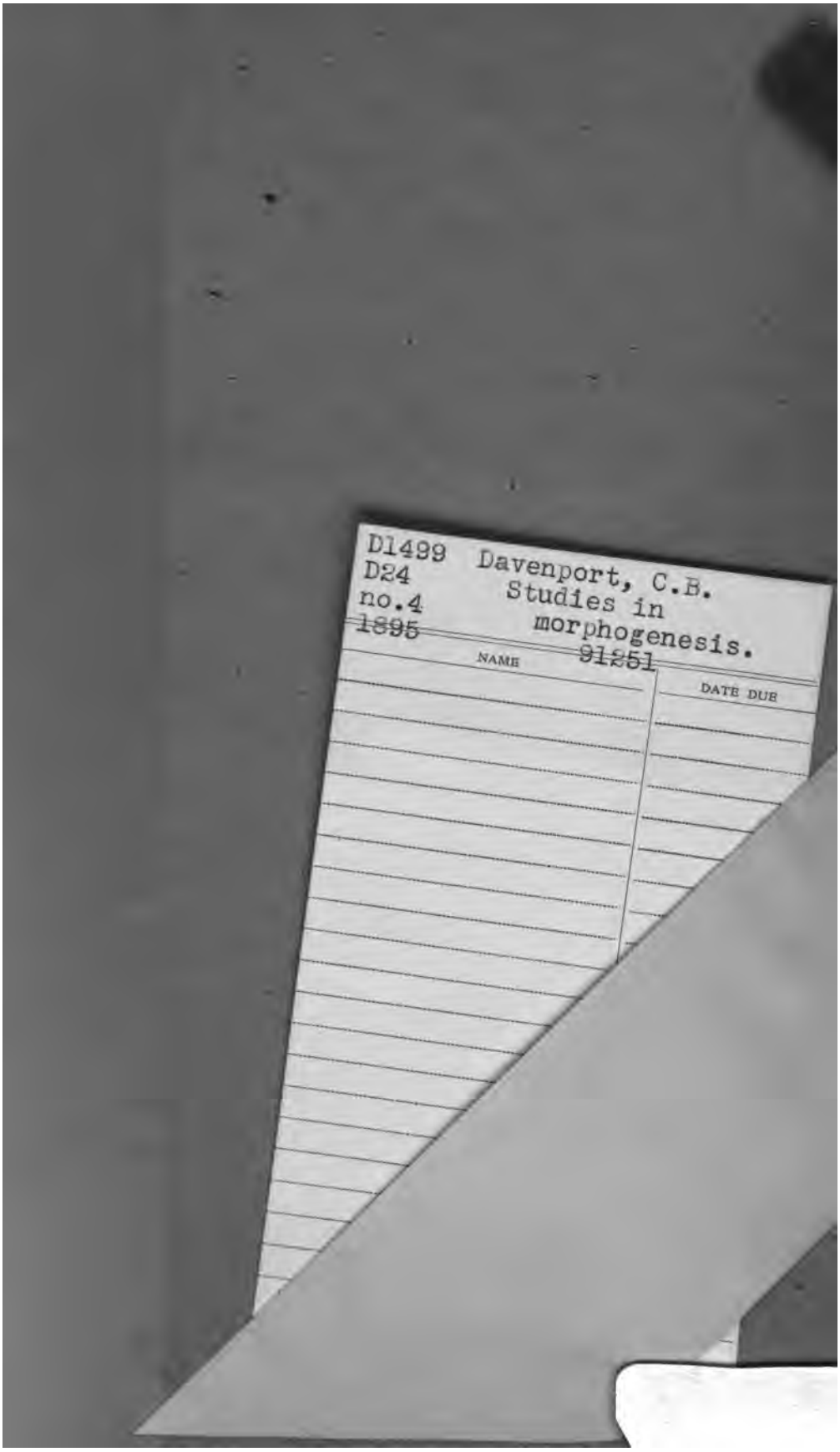
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